REVIEW OF WORK BY PANTEL AND PORTCHINSKI ON REPRODUCTIVE AND EARLY STAGE CHARACTERS OF MUSCOID FLIES.

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The very important recent contribution by J. Pantel, entitled "Recherches sur les Diptères a Larves Entomobies," is the first of three memoirs planned by its author to appear under that head, and bears the subtitle "Caractères parasitiques aux points de vue biologique, éthologique et histologique." It appeared in volume 26, first fascicule, of La Cellule, and comprises 165 pages of text proper, 2 pages of definition of terms, 6 pages of bibliography, 14 pages of explanation of plates, a four-page table of contents, 26 text figures, and 5 well-executed double plates. The text matter is arranged in four chapters, of which the first specially concerns us here, covering much ground upon which I have myself been engaged during the past four years, and adding no little to my own knowledge of the subject of the reproductive and early-stage characters. I should state at the outset that a copy of this publication sent by the author to me in Massachusetts failed to reach me here in Peru, and I had not seen the paper until a second copy reached me late in May, 1911. Thus my paper presented before the Entomological Society of America in 1910, about to be published with additions in the Annals of the Society, has been wholly prepared without knowledge of the results announced by Pantel in this work.

The author presents a table in which he defines ten groups founded on reproductive characters. Primary divisions are made on the form of the egg, the first group having a short, broad egg, to which I should add flattened; the second having a long egg. Two groups are distinguished in the first division, one with a macrotype, the other with a microtype egg. In the second division a group is cut off on the character of the pediceled egg. The remaining seven groups are divided primarily on presence or absence of chitinous terminations of the larvipositor or ovipositor for puncturing the skin of the host. The forms that do not so puncture the skin are then divided on the double-sac or coiled types of uterus, the latter forms separating into those having a delicate uniform chorion and a colored maggot fitted for remaining some time in the open, and those having a dorsally thickened chorion and an uncolored maggot deposited in chorion on host. The colored-maggot forms are divided into those with numerous ovarioles whose maggots are deposited on foliage in vicinity

of the hosts, and those with few ovarioles whose maggots are indicated with a query as probably deposited in the vicinity of the host. Finally, the forms provided with chitinous piercing organs at the tip of the female abdomen are divided into those whose eggs are perceptibly tapered at the posterior end and which are credited with a habit of subcutaneous oviposition, and those whose eggs are the same at both ends and which have the habit of subcutaneous larviposition; the latter being divided again into those with piercer and larvipositor distinct, and those with the two combined.

This grouping becomes in a large measure a true and natural one, but a very considerable number of diverse types are left together in groups I, V, and VI especially. In order to preserve the relative proportions of the whole, these groups need splitting, on whatever characters are available; external adult characters to be used if the eggs, maggots, and reproductive organs do not show sufficient differences, for many of these types are pronounced in the adult. Separate mention of the ten groups follows below, with general mention of the forms referred to them.

Group I.—Species which glue a short flattened macrotype egg to the body of the host. Pantel recognizes the fact that the seventeen forms here grouped by him are of diverse types. While his groups are manifestly not intended by him as taxonomic divisions, I feel confident that proper taxonomic groups can be defined on the characters brought out by such work supported by others judiciously selected from the external anatomy of the adult. Thus we have the following: Phasiidæ: *Phasia crassipennis*, *P. rostrata*, *Cistogaster globosa*, (*Xysta*) *grandis* Egger, (*X.*) *semicana* Egger, and quite possibly *Gymnosoma rotundatum* and *Stylogymnomyia nitens*. Tachinidæ: *Tachina larvarum*, (*T.*) *rustica*, *Tricholyga major*, *Parasetigena segregata*, *Ptychomyia selecta*, *Winthemyia 4-pustulata*, *Nemorilla maculosa*, *Meigenia floralis*, *M. major*, *Thrixion halidayanum*. These further need subdivision into several tribes.

The two Eggerian species that have heretofore been referred to *Xysta* are manifestly not that genus, and may be referred to the new genus *Euxysta*, type *X. semicana* Egger, erected in this paper. (See Group IX for *Xysta*.)

Tachina rustica is the type of the genus *Chætotachina* B. B. Pantel's figure of the female reproductive system in this species shows a very distinct type from that of *Tricholyga* and *Euphorocera* (not *Euph. claripennis* Coq.), which I take to

represent the tachinine type or group-unit. *Chætotachina* has the spermathecal duct extremely elongated and longer than the tubular glands, the latter being not only much shortened comparatively, but also very slender, much more slender than the spermathecal duct; moreover, there is only one spermatheca, according to Pantel, which seems to me most remarkable, since in all of my work I have never found any variation from three. Thus the chætotachinine group is a most distinct one.

The bulb-like enlargement in the spermathecal duct of *Chætotachina* noted and figured by Pantel is considered by him as perhaps a supplementary spermatic reservoir. This might well be the case in this form with only one spermatheca, but I find the same well developed in *Euphorocera peruviana* and *E. minor*, two Peruvian species, both of which have three spermathecæ. I think it more probable that these bulb like swellings of the ducts function alternately as air-exhausts for drawing the spermatozoa down from the spermathecæ through the very long ducts and as expellers for forcing them into the uterovagina. They are very marked and quite spherical in the Peruvian species mentioned, and strike me as being especially comparable to the bulb of a syringe. They may also function as spermatozoal inhibitors during copulation.

Of the forms above mentioned, so far as known, only *Meigenia* and *Thrixion* have a uterus in my sense, which is termed by Pantel "utérus incubateur" and "organe incubateur", and by Dufour "réservoir ovo-larvigere." Pantel considers the uterus present in all forms; I consider it present only in those forms which incubate the eggs. The corresponding organ in those forms which do not incubate the eggs I call the uterovagina, which has no incubating but only a fertilizing combined with a vaginal function; it thus can not properly be called either vagina or uterus, since it combines the functions of the two. The vagina is the more or less well-marked termination of the incubating tube or sac; thus the uterus plus the vagina in the incubating class are homologous with the uterovagina of the non-incubating class.

Pantel records his belief that incubation of the eggs in *Meigenia* and *Thrixion* is probably to be considered exceptional. I can hardly agree to this. I have found eggs in a number of these forms sufficiently developed to show the cephalopharyngeal skeleton of the maggot, and further the elongate coiled uterus would not be present, I believe, unless for the purpose of incubation. Similar incubation is known

to occur normally in *Gastrophilus* and *Hypoderma*, and probably in other forms with thick chorion, as *Cuterebra* and *Dermatobia*.

Pantel points out and accounts for the mistake of Neilson in claiming larviposition for *Tachina larvarum*. Evidently the maggots which Neilson mistook for *larvarum* were destroyed by *larvarum* maggots hatched from the eggs covering the hosts, the *larvarum* maggots themselves being overlooked but the *larvarum* flies reared. This illustrates well what serious confusion may result during investigations that seem well guarded.

The form mentioned by Pantel as referred by me with doubt to *Hemimasicera* is *Cyclotaphrys anser* T.

An important point brought out by Pantel is that of accidental viviparity. Von Siebold has recorded such for *Calliphora vomitoria*. Pantel states that he has noted the same condition in *Euxysta grandis* and *Paraseligena segregata*. While I believe that this phenomenon may actually occur at times, I feel that the greatest caution is necessary in the determination of such individuals, which may in some cases represent other types very similar in external characters. Portchinski's work noted further on, while perhaps correct as to determinations, has an important bearing on this point.

Another point of interest brought out by Pantel's work is that the ovarioles of the muscoid flies are without alternate nutritive cells. I have independently noted this fact. There is a terminal chamber present surmounted by a filament, rather than a terminal filament alone, as in the ovarioles of Thysanura and Orthoptera; but this chamber, while perhaps nutritive in function, is not connected with each ovum by a separate strand-like duct as in the more specialized type of ovariole. I have noted this uniformly in many cases, and it shows throughout Pantel's figures of his ten groups.

In view of the more or less complete development, and oftentimes escape from the chorion, of the maggot in the uterus in a great part of the Muscoidea, it becomes clear that we must in some manner distinguish between oviposition and larviposition. In many cases the fully developed maggot is deposited in its chorion. This is the case with all the leaf-ovipositing species, or the forms with microtype egg. It is doubtless often the case, as Pantel suggests, with forms hitherto supposed to hatch the eggs or liberate the maggots in the uterus, these being deposited in their delicate and transparent choria, as I have several times observed with *Almugmyia arida* and *A. major*, two Peruvian species, the maggots immediately mak-

ing their escape from the chorion and starting away in search of hosts. I have noted the same with *Varichæta ruficauda* in Massachusetts and with *Sarcophaga* in Peru. I believe that it will be at once most convenient and most truly representative of the actual conditions to consider the deposition of all tough or thick chorion eggs as *oviposition*, whether or not they contain the more or less developed maggot; and the deposition of maggots, whether naked or enveloped more or less fully in a delicate chorion, as *larviposition*. The first are always specially provided, either by flat ventral surface, by pedicel, or by heavy chorion carrying an abundance of cement (as in the cuterebrine flies), for outside deposition and attachment to surfaces as eggs. The last are not so provided in any way, the intent of the act in their case being certainly the deposition of living maggots for immediate activity. The membraneous base by which the maggots of the leaf-larvipositing forms are attached to plant surfaces probably consists of a part of the chorion, or perhaps the vitelline membrane, or both, which adheres to the anal end of the maggot at birth, being thus made use of by the maggot certainly at times, though the latter may leave this base in search of a host. The subcutaneous deposition of maggots is perhaps normally made in choria. The subcutaneous deposition of eggs, to be noted farther on, presumably made as eggs without any development of the maggot, is indicated only in those forms with an elongate egg and delicate chorion entirely unsuited for external attachment.

Group II.—Species depositing on the food of the host a microtype egg containing the developed maggot and destined to be swallowed. Fourteen identified species are mentioned here, including the following genotypes which I have not yet been able to dissect: *Baumhaueria goniæformis*, *Cnephalia bisetosa*, *Frontina læta*, *Spallanzania hebes*, *Sturmia pupiphaga*.

Myxexorista pexops B. B. is included and stated to have a shortened uterus with slate-gray eggs. It is thus clearly not the genus *Myxexorista*, which is apparently to be considered synonymous with *Zenillia*, and I propose for it in this paper the new genus *Myxexoristops*. *Zenillia libatrix* has black eggs of smaller size, a long uterus, and more numerous ovarioles.

Baumhaueria and *Frontina* both fall in the same group with *Myxexoristops*, so far as the egg, uterine, and ovarian characters pointed out by Pantel go. They may be found ultimately

to need separate tribes, for the wealth of these forms and the variety of type exhibited by them are but little realized as yet.

Ceromasia rufipes B. B. is also included and stated to have a very small black egg, long uterus, and numerous ovarioles. It is certainly not *Ceromasia*, as the genotype, *Ceromasia florum*, has deep yellow eggs of good size. I propose the new genus *Ceromasiops* in this paper for its reception. Moreover, *Ceromasiops rufipes* is recorded as reared from forficulids, which causes Pantel to question whether the microtype eggs are always deposited on foliage. No doubt a reservation must be made in this respect, but it is quite safe to conclude that they are normally deposited on the food. The investigation of the host relations of *Ceromasiops* promises to be unusually interesting. But it must be observed that forficulids are not uniformly carnivorous and refuse-feeding. A species has been reported in Tasmania as extremely abundant eating into ripe fruits, and others have been found eating the buds of plants.

Brauer's record of *Gonia* parasitic in bees is based, I believe, on Zetterstedt's original record. *Gonia* has been reared in numerous cases in North America from noctuids. The Zetterstedt record may perhaps have been due to infested noctuid caterpillars crawling into *Bombus* nests to pupate. I have not seen the original record.

As to *Spallanzania hebes* having been reported viviparous by Dufour, it may exceptionally happen that a fly should contain in the lower part of the uterus overripe eggs, so to speak, or maggots in chorla that have been carried overtime, from lack of finding suitable places for oviposition, and which may burst from their chorla on the least provocation. The mere handling of the fly may cause this. I have noted the maggots burst from the chorla during dissection of dried specimens of *Blepharipeza* and *Gonia* that have been relaxed, merely as the result of the mechanical effects of manipulation.

A most important point abundantly brought out in Pantel's work is the fact that the female reproductive system in the forms with uterus exhibits very different characters before and after the descent of the eggs. Many forms which possess a very long, coiled uterus at the full stage of gravidity show the uterus practically undeveloped at time of issuance from the puparium and until the descent of eggs from the ovaries has become well inaugurated. This may apparently go so far as to be very misleading, as I have shown with *Gonia*, provided I have not confused two distinct forms, individuals with a short uterus containing fully developed maggots. The one type shows a short uterus in only one or two coils, with very

short oviducts and very large ovaries; the other a uterus in five or six coils, with long oviducts and smaller ovaries. Although I have so far been unable to find differences between either the flies or their eggs and maggots, I am not yet certain of their identity. The difference in the length of the oviducts and the size of the ovaries seems too great to explain by descent of the eggs contained in the uterus, while there are also quite important differences in the relative length of the tubular glands and the spermathecal ducts. The whole matter serves to emphasize the necessity for much care and judgment in the study of uterine characters. The delayed uterine development might be thought to afford a clue to the age of uterine specialization, indicating its comparatively recent acquirement. But it is evident, as suggested by Pantel, that the shortened condition of the uterus is essential to successful coition and the free passage of the male fluid into the spermathecæ. Therefore full uterine development is delayed to allow of copulation.

In this connection the author points out a very serviceable criterion, which is most conspicuous during dissection of the forms with much uterine development, and which serves to indicate such forms even in the newly issued flies before the descent of the eggs and the elongation of the uterus have begun. This is the fact that such forms have the uterus abundantly supplied with masses of minute tracheæ. These positively indicate incubation of the eggs and development of the maggots, and are often very troublesome by binding the coils and other reproductive organs into a close tangle.

Pantel calls attention to the idea advanced by Portchinski that in *Calliphora erythrocephala* only one egg in each ovariole develops. This is, I feel sure, a wholly mistaken idea. It may happen in countries with an extremely short breeding season, as in northern Russia perhaps, but in more southern climes it can hardly be the case. All muscoid flies may be easily divided into two grand categories on the character of continuous or discontinuous development of ova in the ovarioles. *Calliphora* belongs in the latter category. One set of ova develops at a time, the set being composed of the lowest ovum in each ovariole. When these are fully formed, and the fly has been fertilized, they are rapidly deposited in the case of *Calliphora*, *Musca*, *Stomoxys*, etc. In the case of *Sarcophaga*, *Metopia*, etc., the set when fully formed descends rapidly and practically at once into the uterus, where all develop together. Practically always the eggs or maggots in the uterus of these forms are all at the same stage of develop-

ment. I have seen exceptional cases, but they are rare. When the maggots are fully developed they are rapidly deposited. As the maggots approach full development, another set of eggs forms in the ovarioles, and these descend as soon as the uterus has been emptied. I have found the ovaries filled with a set of full-sized eggs and a few perfect maggots in the uterus at the same time, showing that larviposition of one set of maggots was in progress. The leaf-ovipositing and leaf-larvipositing forms belong in the other category, where continuous and successive development and descent of eggs, development of maggots, and oviposition or larviposition take place, the latter depending only upon the finding of suitable conditions.

This second group of Pantel corresponds perfectly to my leaf-ovipositing forms, and seems a most compact and well-defined group, embracing all the microtype egg forms known, and easy of definition by dissection. Nevertheless, the indications are that at least some of these groups are of independent origin from the main stock, and it is quite probable that we shall ultimately find that the group is merely a collection of stocks of diverse origin. I have found types of slender, elongate, more or less pointed microtype eggs, as mentioned in my last paper, and many forms with a deep yellow instead of black or gray chorion, none of these having appeared in Pantel's material.

Group III.—Species extruding large and robust larvæ known as ordinary flesh maggots. This is the group of the sarcophagine, metopiine, etc., flies and their allies, a very natural one characterized by the double-sac form of uterus, termed by Pantel very aptly a twin-pouch incubator. The author does not distinguish between the cordate and V-shaped types of this form of uterus, which I have pointed out.

Pantel's dissection of *Macronychia agrestis*, the type of the genus, makes its reproductive system now for the first time known. The discovery that it possesses, as I had thought probable, the double-sac type of uterus calls for an important change in family nomenclature. Since rediscovering for myself the nature of the sarcophagine uterus, which it appears was described and figured as long ago as 1851 by Dufour, I have felt that the old family Sarcophagidæ should be revived. We are now able to separate these forms definitely from the rest of the Muscoidea. Moreover, other important characters indicate their compactness as a family group, notably the uniformly very generalized type of the cephalopharyngeal sclerites of the first-stage maggot and the position of the posterior stigmata at the bottom of an anal cavity in the mag-

got and puparium. To this family *Macronychia* is now known to belong, and in spite of its divergent facial plate development I believe that it will be found to exhibit the maggot characters just mentioned. It represents an extreme shortening of the facial plate in the sarcophagid stock already begun in the paramacronychiine and especially noticeable in the miltogrammine flies.

Macronychia is thus no longer tenable as the type of the family which I have called, in deference to Brauer, the Macronychiidæ, though realizing that *Megaprosopus* is the real type of the family. This is a natural family group distinguished by the shortened œstrid type of facial plate and the noticeably reduced mouthparts, combined with the presence of true abdominal macrochaetæ. The exclusion of *Macronychia* makes the group a more natural and easily defined one on external adult characters. *Aulacocephala* perhaps belongs here, and *Neophyto* probably goes in the Sarcophagidæ. As *Megaprosopus* is typical of the group, the family may now properly be called the Megaprosopidæ.

In a paper now in preparation I am discussing family characters and reviving both the Sarcophagidæ and Dexiidæ as families, though in a new sense, the Sarcophagidæ standing as above outlined, and the Dexiidæ forming a group with a facial plate, of which *Dexia* is typical. The possession by *Macronychia* of the megaprosopid type of facial plate and the double-sac type of uterus seems to indicate that the latter specialization is of longer standing than the shortening of the facial plate. *Macronychia* and its allies appear to be double-sac uterus stock that has developed the shortened facial plate by parallelism. The same parallel development shows a beginning in certain muscid if not tachinid stocks, as now restricted, and has proceeded far in the dexiid stock. It has progressed farther in this part of the sarcophagid stock. We thus find a successive shortening of the facial plate from the phasiid through the muscid, tachinid, dexiid, sarcophagid, and megaprosopid stocks to the œstrid type. This specialized facial shortening now seems to postdate the primary differentiation of uterine specialization into double-sac and coiled-gut types.

The Brazilian *Pseudogametes* and the Siberian *Microcephalus* both appear to be remnants of an old mesembrinine stock that has acquired a strong œstrid facies. Both have the mouth-parts much reduced and show evidences of a tendency toward a shortening of the facial plate, which is of very peculiar structure, while the cheeks are wide and concave. The well-developed antennæ have counteracted the tendency to-

ward a shortening of the facial plate. Both forms are densely hairy and *Bombus*-like. These forms should throw much light on œstrid, megaprosopid, and sarcophagid relationships when they are more fully investigated.

Pantel quotes Künckel's observation of a female *Sarcophaga* depositing a maggot in the anus of the Morocco locust, and comments on the recent experiments of Lahille with *Sarcophaga* on crickets. I think there is no doubt that sarcophagid maggots do at times enter sound hosts either by body openings or through less chitinized parts, but in any event, though to all practical purposes true parasites, they live rather as scavengers in the host, as pointed out by Pantel. They have formed no habit of procuring air-supply through the skin or tracheæ of the host, as have the truly specialized parasites.

Group IV.—Species which deposit naked maggots or maggots in choria in the path of the host. This comprises the forms which larviposit upon plant surfaces in proximity to the host. It is a large and natural group of subfamily rank, easily dividing into at least nine group-units of tribal rank on maggot and adult characters. All possess a long, coiled, strap-like uterus in which develop colored maggots whose dorsum and sides are covered with minute subchitinous plates.

Pantel mentions that Réaumur described the uterus of *Echinomyia* in 1738, but does not state that he also gave an extremely recognizable figure of it. I believe that the species was *Echinomyia grossa*, which is a most prolific form and has an immense uterus 60 mm. long. I consider Réaumur's estimate of 20,000 maggots in one uterus, however, as rather too high. My own numerous dissections in this group have shown this species and the North American *Archytas hystricodes* to be the most prolific, but in no case have I been able to estimate a uterine content of more than 8,000 to 10,000 eggs and maggots, and this is much above the average. Yet this may exceptionally be exceeded by large flies which have not found suitable conditions for larviposition.

One century after Réaumur's work, in 1838, von Siebold enlarged upon this type of uterus, publishing a most important paper upon these forms. These two authors and their publications, with Sasaki's work on the leaf-ovipositing *Crossocosmia* in 1887, and Portchinski's work in 1885 on coprophagous and necrophagous forms, mark prominent epochs in our knowledge of muscoid reproduction and early stages. Since 1907, greatly renewed interest in this subject has sprung up, as shown by the published work of Hewitt on *Musca*, that of Pantel, Neilson, and myself on the general subject, and that of Austen, Roubaud, and others on *Glossina*.

Pantel figures some of the types of colored armature in the maggots of the present group, and calls attention to the similarity of *Steiniella*, but it should be observed that the armature of the latter is not of the *Varichæta* or *Micropalpus* type. *Steiniella* is approached in armature by *Glaucophana*, both possessing spined plates, but neither form falls in the present group.

The author questions whether the maggots of this group are always deposited on plant surfaces, and not sometimes directly on the host. The observations of Marchand are cited, who claims to have observed *Eupeleteria fera* deposit maggots on the host at the entrance of the spiracles. However this may be, I can only say that the flies of *Eudoromyia magnicornis* which we handled at the Gipsy Moth Laboratory manifested the greatest alarm when they found themselves in *close* proximity to caterpillars, but deposited their maggots on the leaves and stems in the general vicinity of the caterpillars, though always at a respectable distance from them, and at least in certain cases on the fresh silken strands left by them in traversing the plant surface to and from their nests. The caterpillars used were *Hyphantria* and *Euproctis*, which make webbed nests. Both the alarm of the flies when brought face to face with the hosts and the specialized armature of the maggots indicate that larviposition on the host is abnormal. If exceptional cases occur, each must be individually sought for the reason.

Group V.—Species depositing naked maggots or maggots in chorια probably in the vicinity of the host. This is a most instructive group, but a heterogeneous one. It is a collection of extra-leaf-larvipositing forms with colored maggots. Five genera are mentioned: *Bigonichæta*, *Erithorix* (*Olivieria*), *Glaucophana*, *Macquartia*, and *Myiocera*, the maggots of none of which was before known to me, and all of which are of the greatest interest as throwing important light on the host relations of these forms. To these may be added *Ophirion*, *Steiniella*, *Gymnochæta*, and *Phasiopteryx*. No two of these nine genera probably fall in the same ultimate natural group-unit, while two families and four subfamilies are represented among them. All seem fitted to search for their hosts in the open or subopen.

Group VI.—Species depositing naked maggots or maggots in chorια on the body of the host. Thirteen species are here named, all having uncolored maggots, nevertheless forming a heterogeneous assemblage. The author has evidently considered that these maggots, because they lack colored arma-

ture or chitinization for the protection of the integument in the open, are necessarily deposited on the body of the host. But there is a considerable class of hosts to which the fly is denied access, due to the nature of their habitats within substances that the fly can not penetrate. Such are wood-boring grubs within the trunks of trees, white grubs and others beneath the surface of the soil, weevil grubs and others within the various fruits of plants, borers and miners within the fleshy parts of plants, and various other protected hosts of a similar nature. The ingenuities of parasitism have triumphed over the isolation of these hosts, and the flies deposit their maggots as near to them as they are able to approach, leaving the rest to their progeny. The maggots reach the hosts for themselves either by penetrating the soil, following the galleries of borers, or burrowing into the substances of plants and their fruits, in short following the hosts where the flies cannot enter. As these maggots are not exposed to open conditions they do not need integumental specialization. Thus certain of the forms here grouped by Pantel, as for instance *Leskia aurea*, do not necessarily larviposit on the host. The true dexiine flies exhibit the largest number of forms parasitic upon hidden hosts, such as white grubs, woodborers, and weevil grubs in various pods, nuts, and fruits.

Pantel's consideration of the rôle of the maternal organs in intrauterine incubation is of interest. He considers the possibility of the tubular glands functioning as suppliers of nutriment, and the possibility of an osmotic supply through the walls of the uterus from the maternal blood. I believe that both of these methods may occur in the case of *Glossina* and other forms that carry the maggot through one or more stages in the uterus, but I do not think they occur during the development of the embryo. The uterus probably acts merely as a mechanical container during the latter period. The nutritive supply which provides for the development of the ova in the ovarioles must be derived either directly or indirectly from the blood, perhaps through the fat-body; once formed and fertilized, the egg probably contains all the elements and nutritive supply necessary for the full development of the maggot.

Group VII.—Species introducing into the body of the host, by means of separate instruments of perforation and injection, naked maggots or maggots in choria. This is the group of *Compsilura* and its allies, having the habit of subcutaneous larviposition. It is a very natural group, but with only the

taxonomic rank of a tribe. I am inclined to consider it a group-unit of the subfamily Phaniinæ. In addition to *Compsilura* and *Dexodes*, Pantel gives here *Vibrissina demissa*. I can add *Eucelatoria* and American species of *Vibrissina* or closely allied forms, besides *Phorocera doryphoræ* Riley, whose generic reference is yet in doubt.

We are indebted to Pantel for first correctly defining and figuring the peculiar structure of the larvipositor and piercer in *Compsilura concinnata*. I have verified his results in a dissection of *Eucelatoria australis*. The piercer and larvipositor are separate structures, the latter fitting so closely into the base of the former dorsally and being so little chitinized ventrally as to obscure its form. There are heavy, thick muscles at the base of the piercer which move it, these being attached to the last ventral plates. The walls of the end of vagina possess muscles also for injecting the maggot. The larvipositor is a tapering tube, the main chitinized part forming the roof, the rest being membranous, with only a narrow longitudinal chitinous piece or rod forming the floor support and keeping the tube stretched properly below. The larvipositor is everywhere thickly studded inside with short, sharp spines or spine-like tubercles, which show conspicuously through the membranous portions and are for insuring the exit of the maggot, as they all point posteriorly. The propulsive force is furnished by the vaginal muscles.

The tip of the larvipositor certainly enters the puncture in the skin of the host made by the piercer. The piercer is grooved on its upper surface, the larvipositor lying in this groove. The upper or main chitinous portion of the larvipositor is rather sharply pointed at tip to insure entrance within the puncture, the tip of the ventral supporting rod of the membranous part less so, these two pieces doubtless not opening or separating at their tips until both are well within the puncture, their separation in that position opening the tube for the proper egress of the maggot therefrom within the skin of the host.

I find no mention by Pantel of the peculiar spinigerous ventral carina of the female, characteristic of all these forms, which appears to be primarily adapted for preventing the skin of the host from slipping forward during the forward thrust of the piercer, this action at the same time facilitating the opening of the puncture as widely as possible. The spines of the carina are directed posteriorly. The posterior part of the carina also receives and protects the sharp point of the piercer, the latter being so perfectly introduced within it

and approximated to the fifth ventrite during a state of rest that it becomes almost invisible, even on close inspection with a lens.

Group VIII.—Species introducing naked maggots or maggots in choria into the body of the host by means of a combined instrument of perforation and injection. *Cercomyia curvicauda* is cited as the sole representative of this group. It is stated to have a uterus and maggots very similar to those of *Compsilura*, with the eggs and maggots in single file in the uterus. The terminal apparatus of the female abdomen is believed to signify subcutaneous larviposition by means of a slender organ which acts at the same time as piercer and injector.

Group IX.—Species deprived of incubating apparatus, but provided with chitinous ovipositor of variable form, apparently for introducing the undeveloped eggs into the host. The author here places three subgroups, the first including *Alophora*, *Hyalomyia*, and *Xysta*; the second comprising the Conopidæ, and the third doubtfully including *Ocyptera*. The Conopidæ are taxonomically outside of our subject, but their probable possession of such habit is of much interest. They are simply grouped here by the author for convenience of treatment from a parasitic point of view.

A dissection of *Alophora* which I made in 1908 suggested to me the very possibility here outlined by Pantel, that of subcutaneous oviposition. I have mentioned in my last paper that the female possessed in this case a piercer-like organ curved in the opposite direction from that of *Compsilura*. The eggs were undeveloped. Not having opportunity to dissect further material so as to demonstrate conclusively the uterine characters, I have been loath to advance the theory of subcutaneous oviposition. Pantel, however, has carefully dissected *Alophora*, *Hyalomyia*, and *Xysta*, and pronounces them without incubating uterus, thus excluding the possibility of larviposition. This being the case, it seems quite evident that subcutaneous oviposition is here the habit, since, as the author points out, the eggs are totally unadapted for external attachment to the host. Pantel deserves the credit for first suggesting if not establishing the existence of this type.

I can add that *Hemyda aurata* and *Penthosia satanica* both appear to have the same peculiar eggs, and I believe it probable that both have a subcutaneous oviposition habit.

I do not think that *Ocyptera* comes here. A female which I dissected in 1908 exhibited a uterus containing elongate eggs, some of which showed developing maggots.

It seems hardly possible that *Alophora* and *Hemyda* can belong to the same subfamily. I believe that *Alophora* is to be grouped with *Phasia* in the Phasiinæ, notwithstanding the very diverse reproductive characters of the two. *Hemyda* and *Cercomyia* I consider members of the subfamily Phaniinæ, in which I am also inclined to include *Compsilura* and its allies. All three, however, have certainly much affinity with the pseudodexiine and pyrrhosiine types, which I unite in the subfamily Pseudodexiinæ.

Group V.—Species depositing on the host a pediceled egg in which the maggot is already well developed. The author cites *Parexorista cheloniæ* as the sole representative. Nielsen has shown in his last paper (1911) that *Carcelia* has the same egg. Pantel considers both species as *Carcelia*, but it seems to me that *cheloniæ* is generically distinct on adult characters if not on others.

This group I consider as forming a tribe of the subfamily Hemimasiceratinæ.

It seems quite certain that normally the egg is not deposited until the maggot is well advanced in development, as with *Gastrophilus* and *Hypoderma* among pediceled-egg forms and *Meigenia* and *Thrixion* among flat-egg forms. But we noted positively at the Gipsy Moth Laboratory that both *Parexorista cheloniæ* and *Carcelia gnava* deposited undeveloped eggs, which I must consider exceptional.

A number of species of uncertain reference are mentioned by Pantel, which are of interest. They are as follows:

Ceromasia florum the author thinks may belong with *Blepharidea* in his Group VI. He had only undeveloped females for dissection. A dried specimen dissected by me, determined as this species by Brauer and von Bergenstamm, showed yellow microtype eggs. It thus belongs in Pantel's Group II, with the leaf-ovipositing forms.

Exorista westermanni the author believes to possess a microtype egg, and to have similar characters to *Frontina*. I hope that someone will soon dissect the type species, *crinita* Rdi., and thus establish the status of the genus *Exorista*. I have found the most widely divergent reproductive characters—flattened-oval macrotype eggs deposited on host, microtype eggs deposited on leaves, elongate maggots developing in uterus and deposited naked or in choria on or near host—in specimens which possess the external characters ordinarily considered as defining the genus *Exorista*. *Phorocera* similarly needs establishing on its type species *cilipeda* Rdi.,

which probably has a microtype egg. *Masicera* is already established as a microtype-egg form. These three genera, as commonly determined on external characters, show all three forms of reproductive habit above outlined. *Sturmia* is another mixed-reproduction genus, as heretofore accepted, but its type, *pupiphaga* Rdi., has been shown by Pantel to have the microtype egg, and thus its status is now established. Brauer and von Bergenstamm came nearer to separating these forms correctly on external characters than anyone else, and Coquillett came farthest from it.

Microphthalma europæa is mentioned by Pantel as having a very long, irregularly coiled, and convoluted uterus containing elongate irregularly disposed eggs. I have already published the fact that these develop in the uterus to very hairy maggots.

Psalida (*Leucostoma*) *analis* the author refers to his Group IX along with *Alophora* and *Xysta*. I believe that it falls in the Phaniinæ with *Hemyda*, *Penthosia*, and allies. I have noted the remarkable mandibuliform pincers of the female, but have not had material available for dissection.

Siphona cristata is referred to the author's Group VI. Dufour observed that it has an incubating uterus. It is remarkable as possessing only two spermathecæ.

Sturmia atropivora is referred also to Group VI. It is not a *Sturmia*, but has elongate macrotype eggs and probably deposits maggots. It was designated by Mik as the type of his genus *Zygobothria*.

The extremely interesting and instructive details of parasitism and host reaction detailed in Chapters II to IV are outside the province of this review, which is intended only to correlate the work of Pantel and Portchinski with the results so far secured by myself in the investigation of reproductive and early-stage characters that will indicate relationships.

Finally, the author advises me by letter that Kolodkovosky announced in 1909 the discovery of a second pair of glands arising from the vagina, but in what form or forms he does not state. I have not seen Kolodkovosky's paper. Pantel adds that he has not been able to find any indication of such additional glands in his dissections, and I can add that I have not met with any sign of them in my own work.

In this same connection it is fitting to refer back a full quarter century to J. Portchinski's work on necrophagous and coprophagous muscid larvæ published in 1885, and reviewed by Osten-Sacken in 1887, in the Berliner Entomologische Zeitschrift. Several most important points in the reproduction of groups of Muscidæ are there brought out.

Cynomyia, type *mortuorum*, long classed with the Sarcophagidæ and even continued so to the present day by many authors, was shown by Portchinski to belong unmistakably to the calliphorine flies. Its maggots are almost identical with those of *Calliphora*, it is oviparous, and evidently lacks uterus. It thus goes in the subfamily Calliphorinæ.

The reproductive habits in the important subfamily Mesembrininæ are well set forth by Portchinski. *Mesembrina*, type *mystacea*, deposits on dung not over two dozen large eggs, which are 4 mm. in length. These eggs, which look more like small pupæ, hatch in about twenty-four hours into maggots with anal stigmata characteristic of the first stage. These, Portchinski states, shortly change directly to the third stage, entirely omitting the second stage, the stages being identified on the characters of the anal stigmata. The maggot period is very short.

Metamesembrina, type *meridiana*, is larviparous, depositing large maggots in dung. It was investigated in the Crimea. A female was found to contain a large maggot 3 mm. long, and alongside of it an egg of the same size. It was not followed further apparently, but probably has the same habit as *Dasyphora* next to be considered.

Dasyphora, type *pratorum*, was found to have a remarkable style of reproduction, then for the first time made known outside of the *Pupipara*, and thus announced before this habit was known to exist in *Glossina*. One large egg at a time is retained in the uterus, and not only is it developed to the maggot, but the latter is carried through its first and second stages in the uterus and deposited in its third stage on dung. It feeds to some extent before pupating, thus differing from the deposited maggot of *Glossina*, which is said to feed not at all outside.

Here then are several types of reproduction in the subfamily Mesembrininæ, and the most specialized showing a remarkably close approach to that of the tsetse-flies, *Glossina* and perhaps *Glossinella*, which I have considered a group of the subfamily Muscinæ, but which may yet prove to be more closely related with the Mesembrininæ. At all events it is well established by Portchinski's work that the mesembrinine flies, unlike the calliphorine, possess a true or incubating uterus.

Remarkable indeed are the results secured by Portchinski in his investigation of *Musca corvina*, which show beyond doubt that this species is not congeneric with *Musca domestica*. It becomes necessary to found a new genus for its re-

ception, and *Eumusca* is proposed for it in this paper. Moreover the form is indicated as belonging with the Mesembrininæ rather than with the Muscinæ.

Eumusca corvina was found in the north of Russia to deposit not over two dozen large eggs on dung. These eggs are about 1.5 mm. long, not including an elongated curved appendage about two-thirds as long as the egg proper, which acquires a dark color before hatching. The hatched maggot is first stage, and it transforms directly to the third stage, omitting the second stage, in the same manner as *Mesembrina mystacea*. In the south of Russia this species was found to breed in exactly the same manner during early spring and rarely in summer, but almost exclusively in summer it was found to have a different style of egg, lacking the appendage and like that of *Dasyphora*, but proportionately much larger, which it hatches in the uterus, and further carries the maggot in uterus to third stage, omitting the second stage entirely, as before, and practically in this point only differing from *Dasyphora*. I am inclined to believe in Portchinski's observation that two species are not mixed here, but I cannot suppress a strong doubt due to the total difference in the egg. I might admit oviposition under cool conditions and larviposition under warm conditions in the same species, perhaps, provided the form of egg were similar in both cases, and this of itself seems a great deal to assume in these flies. But with the difference in the eggs it seems almost insuperable. Yet the muscoid flies have specialized in all sorts of directions to an extent hardly to be dreamed of by those who have not paid great attention to their study, and for this very reason I do not dare to denounce any observation, however extraordinary, without the most thorough investigation beforehand. The extreme similarity of the two forms in the adult proves nothing, as we know. Thus there is a very large possibility that two forms are confused here, and that the females believed to be *Eumusca corvina* and which carried the maggot in uterus to the third stage, are a distinct form that appears in the south of Russia only after warm weather sets in. *Eumusca corvina* is known to be a northern form of boreal tendency, and is not recorded to my knowledge from more southern regions than central Europe, except in the present instance and excluding a doubtful Egyptian record, but if so the southern form may just as well be distinct. Robineau-Desvoidy describes three species in his posthumous work which were so similar to *corvina* that he acknowledges him-

self uncertain as to their distinctness. One of these might easily be the Crimean and Caucasian form observed by Portchinski as carrying the maggot to the third stage in the uterus. The fact that this form omitted the second maggot stage in utero, on the contrary, makes it possible that both were the same. At all events, *Eumusca corvina* is established as possessing an incubating uterus, and is thus entirely distinct from *Musca*. I believe that it forms a connecting link between the Muscinæ and the Mesembrininæ.

Portchinski further found that *Pyrellia serena* and *Graphomyia maculata* deposit a small number of large eggs, which he states not to exceed 44 in number. Both evidently belong to the Mesembrininæ.

Myiospila meditabunda and *Spilogaster angelicæ* lay not over two dozen large eggs, while *Spilogaster divisa* and *Hylemyia strigosa* are viviparous. The egg of *Myiospila meditabunda* at least has the curved appendage noted in the deposited egg of *Eumusca corvina*. The maggot of *Hylemyia strigosa* develops singly, rarely two at a time, in the uterus and is deposited in its first stage, but as a very large maggot which passes rapidly through its second and third stages. These are all coprophagous and seem to belong in the Anthomyioidea, but may yet prove to have greater affinity with the Muscoidea.

Portchinski also states that what has been called *Dasyphora lasiophthalma* deposits eggs. It is therefore not *Dasyphora*, and may be called *Eudasyphora*. Most of the species of *Hylemyia* deposit eggs, and if the type species, *strenua* R. D., is among these then *strigosa* will need a new generic name. I am perfectly aware that coprophagousness tends toward viviparousness, as witness the case of *Chironomus stercorarius*, now referred to *Orthocladius*, which is coprophagous, and one of the few viviparous Nemocera. Other coprophagous Nemocera, however, appear to retain the habit of oviposition. In any event, such wide deviation in reproductive habit implies at least generic distinctness, if not tribal.

Portchinski's work marks an extremely important epoch in the progress of muscoid investigations.

I give below formal announcement of the new genera mentioned in the preceding remarks, with their type species.

Euxysta, nov. gen.

Proposed for *Xysta semicana* Egger in the sense of Pantel (1910). Believed to deposit flattened oval macrotype eggs on host.

Ceromasiops, nov. gen.

Proposed for *Ceromasia rufipes* B. B. in the sense of Pantel (1910). Deposits small black microtype eggs, presumably on plants but almost certainly on food of host. Has presumably an elongate uterus. Forms have been recorded under this specific name as reared from Forficulidæ.

Myxexoristops, nov. gen.

Proposed for *Myxexorista pexops* B. B. in the sense of Pantel (1910). Deposits large slate-gray microtype eggs, presumably on plants. Has a shortened uterus and a less number of ovarioles than the forms with more elongated uterus.

Eumusca, nov. gen.

Proposed for *Musca corvina* Fab. in the sense of Portchinski (1885) for his egg-depositing form, whose enlarged eggs are provided with an elongated curved appendage and deposited evidently after having been incubated in the uterus.

Eudasyphora, nov. gen.

Proposed for *Dasyphora lasiophthalma* in the sense of Portchinski (1885). Deposits eggs.

HOW EMPHOR DRINKS.

On August 19 I was collecting insects in the marshes of the Eastern Branch, on the outskirts of Washington. At the edge of the marsh some large holes had been dug, apparently to furnish drinking-water for cattle. On approaching one of these water-holes I found large bees rapidly descending directly to the water-surface and others rising from it. The bees alighted unhesitatingly upon the water and rested upon the water-surface with legs spread wide and the wings folded upon the back. In this position the bees usually remained about ten seconds; the proboscis was in contact with the water and they were evidently drinking. New individuals were constantly arriving and sometimes four or five bees rested upon the water-surface at one time. All the visitors appeared to belong to one species, which Mr. Crawford has kindly determined as *Emphor bombiformis* Cresson.

Frederick Knab.